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Edaphical distribution patterns of macrofungal species in deciduous forest of south Sweden

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ABSTRACT

The distribution of the 150 most frequent species of macrofungi in deciduous (beech, oak, hornbeam, hazel) forest of south Sweden was related to the base saturation and organic matter properties of the humus horizon. Totally 228 permanent observation plots (each 500 m^2) were studied, usually for 4 years, in the period 1978-1987.

For the majority (86) of the species, a statistically significant linear relationship was obtained between frequency distribution and a soil variable constituting an integrated function of base saturation and organic matter content of the humus horizon. In 27 species the variability accounted for by the soil variable was > 80%. Only 10-11 species displayed frequency maxima at intermediate values of the soil variable, whereas 46 species had a very wide edaphical range. Species with distinct frequency maxima or an exclusive occurrence at either end of the edaphical range were found in all main functional groups. The sporophore production of most mycorrhiza taxa was distinctly highest in the very acid soils, particularly in the mor podzols.

KEY-WORDS: macrofungi, deciduous forest, beech, oak, hornbeam, hazel, soil, base saturation, humus.

RÉSUMÉ

La distribution des 150 espèces de macromycètes les plus fréquentes dans les forêts décidues (hêtre, chêne, charme, noisettier) du sud de la Suède a été mise en relation avec la teneur en bases et les propriétés de la matière organique de l'horizon humique. Au total, 228 placettes permanentes d'observation, de 500 m^2 chacune, ont été étudiées, en général sur 4 ans entre 1978 et 1987.

Pour la majorité des espèces (86), on a obtenu une relation linéaire statiquement significative entre la fréquence de distribution et une variable de sol constituant une fonction intégrée de la teneur en bases et du contenu en matière organique de l'horizon humique. Pour 27 espèces, la variable sol explique plus de 80% de la variabilité. Seules 10 à 11 espèces présentent un maximum de fréquence à des valeurs intermédiaires de la variable sol, tandis que 46 espèces couvrent une très large gamme édaphique. On trouve des espèces présentant des maximums de fréquence distincts ou une occurence exclusive à chaque extrémité de l'éventail édaphique dans tous les principaux groupes fonctionnels. La production de sporophores de la plupart des taxons mycorrhiziens est nettement supérieure dans les sols très acides, en particulier dans les podzols de type mor.

MOTS-CLÉS : macromycètes, forêt décidue, hêtre, chêne, charme, noisettier, sol, teneur en bases, humus.

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INTRODUCTION

Fungi play a fundamental role in the ecology of forest ecosystems. Much of the decomposition work necessary for a proper mineralization and recirculation of essential nutrients is performed by fungi. Forest trees form ectomycorrhiza with numerous species of the mycoflora, a symbiosis considered to be a prerequisite of a sufficient supply of certain minerals or even of their survival in poor soils.

The edaphical differentiation of the macrofungal flora in European deciduous forest is not well known, in spite of numerous accounts of the mycofloristic composition of forests. Most descriptions have been related to forest types or sociologically defined vascular plant communities and not to the soil properties per se. More or less extensive surveys are available from deciduous forest in, e. g., Poland (GUMINSKA, 1962; LISIEWSKA, 1972; BUJAKIEWICZ, 1981; 1982), Roumania (BARBU, 1979), Czeckoslovakia (SMARDA, 1972), Belgium (DARIMONT, 1973), the United Kingdom (WILKINS *et al.*, 1937), just to mention a few. As a rule, no or only few edaphical data accompany the published descriptions. Any real analysis of relationships between soil properties and fungal occurrence has usually not been performed. Recently, however, several studies on soil-macrofungal relationships in beech forest were published (TYLER, 1984; 1985; HANSEN, 1988).

However, the existence of a decided edaphical preference in many fungi seems to be recognized, though judgements, e. g., in mycological handbooks, are evidently most often based on the general experience of various authors. Opinions sometimes differ to a large extent, which might depend on difficulties in estimating edaphical characteristics without soil analysis or depend on a true variability in the ecological behaviour of a species in various parts of its geographical range. A further reason may be genetic and ecophysiological variability within morphologically defined species. Whatever the reason, there is a need for consistent information of the edaphical behaviour of macrofungi based on descriptive soil chemical and physical data.

Since the difficulties to identify most macrofungi from hyphal characteristics seem almost insuperable, an assessment of sporophore frequency and production is the only way to describe the macrofungal composition of an ecosystem. However, only a limited number of all species present in a forest stand produce sporophores simultaneously. Therefore, the stand has to be examined several times for several years, if a reasonably complete picture of its fungal « community » is to be obtained. A question of great concern is to what extent sporophore frequency reflects the abundance and activity of the mycelium. Detailed accounts of early successional stages of the mycoflora associated with birch (Betula spp.) indicates that a close relationship is highly probable (FORD *et al.*, 1980; LAST *et al.*, 1984). HERING (1982) concludes that fruit bodies are useful indicators of the complement of species present, and of the distribution of a given species across a site. Evidence has also been demonstrated in several other studies (e. g., AUGUSTIN, 1974; SWIFT, 1982; NANNFELDT, 1986) for the possibility of defining spatially separate mycelia using the sporophore distribution in repeated, detailed analyses of a site. AGERER (1985) found a close relationship between mycorrhiza abundance and sporophore production in a beech forest soil. Though exceptions may occur, it seems most likely that abundance and distribution of sporophores is a good measure of mycelial abundance and distribution within and between forest sites, provided several years

are considered to neutralize aberrations in climate or possible inherent patterns in fruiting behaviour.

The objectives of this study are to analyse and summarize information on soil-fungal relationships from the sporophore occurrence in a large number of permanent observation plots in south-Swedish deciduous forest. Base saturation, pH and organic matter contents were used to characterize the humus layer of the plots and the sporophore frequency to describe the edaphical distribution of the 150 most regularly occurring macrofungal species.

MATERIALS AND METHODS

Study area and ecosystems

The deciduous forest of the south Swedish province of Scania, an area situated just south of the border of naturally occurring coniferous forest in Scandinavia, was the object of the study. Observation plots ($n = 250$, area 500 m^2, usually 20×25 m) were selected in pure stands of beech (*Fagus sylvatica* L.), oak (*Quercus robur* L., in a few cases *Q. petraea* Matt.) and hornbeam (*Carpinus betulus* L.) stands, as well as in mixed oak-hazel (*Corylus avellana* L.) and oak-hornbeam stands. The plots were distributed over most of the province (an area of ca. 10,000 km^2) so as to represent the great edaphical variability of these ecosystems as closely as possible. Descriptive surveys and analyses of the vascular plant composition of the stands have been published elsewhere (Tyler, 1984; 1985; 1987; 1989*a*; Rühling & Tyler, 1986).

Being the normal condition in forest soils of south Sweden, most of the sites were characterized by definitely light-textured, mainly sandy soils with a low clay content ($\leq 5\%$) of the top 0-5 cm layer in 79% of the observation plots. A limited number, 8% of the plots, had $> 10\%$ clay. The clay variable was considered in previous studies on soil-fungal relationships, though found to explain but little of the variability of fungal sporophore occurrence (cf. Tyler, 1985; Hansen, 1988).

All the studied sites are situated between 30 and 150 m (mainly 50-100 m) above sea-level, on horizontal ground or gentle slopes variously oriented with respect to points of the compass. Sites with an apparent bad drainage (high water table) were avoided, as were sites where cuttings or other visible interference had occurred within about five years prior to the observation period. Young stands (age < ca. 50 yr) were also rejected. During the course of the study, 22 plots had to be excluded owing to severe disturbance, leaving 228 plots to be considered.

All sites were unlimed, unfertilized and ungrazed. The soils varied from well-developed podzols on tills derived from archaean siliceous rocks over degraded highly acidic brown forest soils, to less acid brown forest soils with a well-aggregated mull horizon, usually of a sedimentary rock origin. No soils with remaining calcium carbonate in the A horizon were included, being essentially lacking nowadays in the forests of south Sweden in spite of the limestone bedrock in parts of the region.

Taxa considered

The study is based exclusively on macrofungi forming epigeic sporophores, soil and wood/bark inhabiting species belonging to the following groups:

Cantharellaceae
Clavariaceae
Clavulinaceae
Ramariaceae
Hydnaceae
Dacrymentales (Calocera)

Phallales
Nidulariales (Crucibulum, Cyathus)
Lycoperdales
Sclerodermatales
Boletales
Agaricales s.l.
Russulales
Pyrenomycetes (Cordyceps, Xylaria)
Pezizales

Microscopic and staining methods were utilized whenever necessary or advantageous for species identification. The main floras used were BRESADOLA (1980), DENNIS (1978), LANGE (1935-1940), MOSER (1978), NEUHOFF (1956), SCHAEFFER (1952) and SINGER (1965). The nomenclature follows MOSER (op. c.) and DENNIS (op. c.), unless otherwise stated.

In a few cases, related though apparently not identical taxa were sometimes impossible to separate in a consistent way due to the occurrence of sporophores with morphologically intermediate characters in this region. These are *Amanita excelsa/spissa*, *Clitocybe dealbata/rivulosa*, *Cortinarius paleaceus/hemitrichus* and *Russula alutacea/olivacea*. It may be argued whether these often apparently inseparable taxa should be treated as distinct species. Though usually identified to species level, numerous edaphically related but infrequent *Inocybe* taxa and the several scarce *Agaricus* taxa were united as *Inocybe* spp. and *Agaricus* spp., respectively, to make a general characterization possible. Highly ephemeral sporophores of small *Coprinus* species were only distinguished to genus.

In discussing their edaphical behaviour, the 150 species/taxa considered were distinguished as belonging either to mycorrhizal or decomposer genera. As the knowledge of the functional properties of many species are still quite limited, no attempt is made to discern functional intermediates, e. g. facultative mycorrhiza formers, which may occur to some extent in the material.

METHODS

Each of the observation plots was studied for 3-5 (usually 4) years in the period 1978-1987. All parts of the edaphical gradient was well represented every year. The sporophore searches were performed on 20. July-20. October with an emphasis on the season of most abundant sporophore production (usually 15. August-15. October). The duration of each search was 20-30 minutes, the variability being due to sporophore quantity and the structure of the field layer vegetation. All sporophores (or clusters of sporophores in some wood decomposer species) were counted or (at plentiful sporophore production) estimated. Sporophores were removed when necessary for macro- and microscopic species identification. Each observation plot was searched for 10-15 (usually 12) times or totally 5-6 hours during the years. Thus, the study is based on at least 1,200 effective hours of field work.

For a general characterization of the edaphical properties of the observation plots, topsoil (main part of the humus layer, 0-5 cm depth) was sampled twice, in two different years. Samples from ten regularly distributed points within the 500 m^2 area were pooled to one bulk sample of $10 \times 192{,}5$ cm^3. Material passing a 6 mm screen was used for determination of pH (0.2 M KCl, soil : solution weight ratio 1 : 5), base saturation percentage (ammonium acetate method, pH 7.00; cf. TYLER, 1985) and organic matter percentage (as loss on ignition). The difference in the material as a whole between the two samplings was 0.09 pH_{KCl} units, 1.2 base saturation % units and 0.21 organic matter % units. Though of minor importance to the results these differences reflect the combined effects of interannual variability and sampling as well as analytical errors. The means of the two samplings are used throughout this study.

EDAPHICAL SITE CHARACTERIZATION

The base saturation and organic matter content are interrelated in such a way that it is possible to characterize the humus layer of a site using these parameters. A curvilinear relationship is displayed

when organic matter % is plotted against base saturation % (Fig. 1) and one new variable composed of these two parameters is easily discerned. The sites along this integrated variable were classified in ten groups composed of an equal number of sites (n=22-23); group 1 representing the most acid mor portion of this edaphical gradient, group 10 the least acid mull at the other end of the gradient. The delimitation of these SOIL groups is evident from Figure 1.

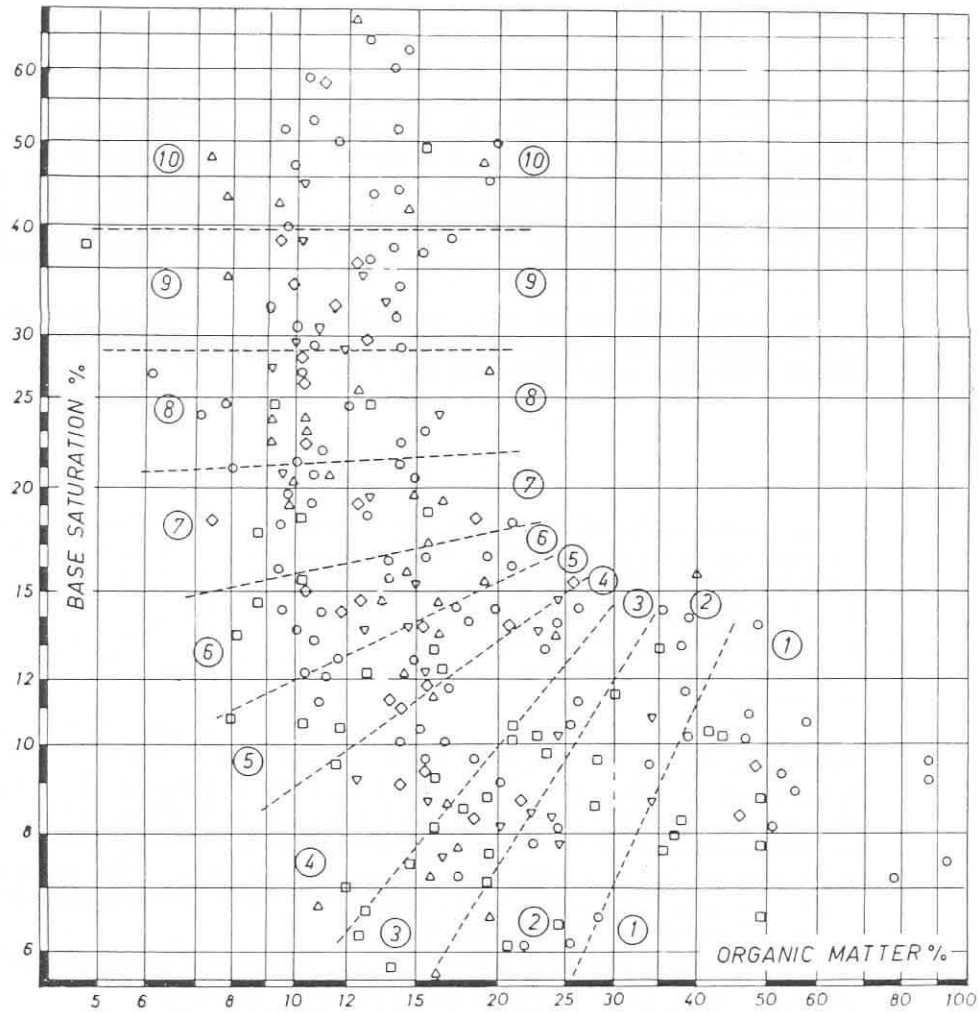

FIG. 1. – The relationship between the organic matter content (% dry weight) and the base saturation (% C.E.C.) of the humus layer of the 228 sites. An integrated variable is discerned and the sites classified in ten groups (1-10) along this variable, each group composed of an equal number of sites. Symbols used, forest dominated by: □ oak, ◇ oak/hazel, △ hornbeam, ▽ oak/hornbeam, ○ beech.

Being the probably best simple expression of the mor-mull direction of variation this classification was used to characterize the edaphical behaviour of the 150 species considered. The classified variable

proved to be closely correlated with pH_{KCl} ($r = 0.966$, $p < 0.001$) and is, consequently, a good measure of the acidity of the deciduous forest soils (cf. TYLER, 1989*a*). However, in trying to replace this classified variable by pH_{KCl} the significance level of the relationship with sporophore distribution decreased in several species, partly due to a higher random variability of the pH_{KCl}. The total $pH_{0.2\ M\ KCl}$ range measured was 2.8-5.1. The occurrence of all the species was defined as the presence (frequency %) in each of the ten soil classes.

CLIMATICAL AND METEOROLOGICAL CONDITIONS

The climate of Scania is cool-temperate, suboceanic. The annual precipitation sum averages 600 mm, the mean temperature of July being +17°C and that of January −1°C. Annual precipitation figures were close to average for the region in most of the years, 1978-1987, except in 1980 and 1981, when the precipitation sums were about 20% above normal, according to official Swedish statistics. The precipitation of July-October was comparatively low in 1979 and in 1983 (only 62-64% of normal), high (120-125%) in 1980, and 1981 and close to normal in the other 6 years. The July temperature varied between +14.5°C in 1979 and +18.3°C in 1983, that of January appreciably more, between +4,3°C in 1983 and −6.3°C in 1987.

The decade of 1978-1987 has consequently offered much of the meteorological and climatical variability typical of south Sweden. The long duration and the cumulative character of the study will therefore ensure a good representation of the macrofungal flora of this region.

RESULTS

A general outline of the relationship between fungal frequency and the edaphical grouping along the composite base saturation/organic matter variable (in the following named SOIL) is illustrated (Figs. 2-3). The majority (86 out of 150 taxa) display a statistically significant linear relationship to SOIL, positive in 35, negative in 51 cases. In these 86 taxa more than about 40% of the variability in occurrence is accounted for by SOIL. In 27 taxa the variability accounted for attains or even exceeds 80%.

The position along the *X*-axis in Figures 2-3 represents the centre of the distribution of each taxon in relation to SOIL, an equal number of presence sites being found on either side of the number symbol indicated in the graphs. This means that, e. g., taxa Nos. 112, 113 and 51 (see Table I) display an extraordinary preference for high SOIL values (the least acid mull), Nos. 8, 14 and 37 for low SOIL values (the most acid mor). Sometimes curvilinear relations give a low estimate of the real variability accounted for, mainly in taxa with an extreme preference for either end of the SOIL axis.

A more detailed account of the frequency distribution of selected species along the SOIL axis is given in Figure 4. Six edaphical distribution types (explained in Table I) have been discerned in order to increase the lucidity of the data.

Type A a. — A pronounced maximum at low SOIL values is evidenced by 25 taxa, particularly frequent ones being *Amanita citrina*, *Galerina hypnorum*, *Lactarius theiogalus*, *L. camphoratus*, *Mycena cinerella*, *Nolanea cetrata*, *Russula mairei* (in beech forest) and *Mycena epipterygia* (in oak forest).

Type A b. — A less pronounced, though usually statistically significant maximum at low SOIL values is demonstrable in 27 taxa. Belonging here are several of the most frequent and abundant species of the south-Swedish deciduous forests.

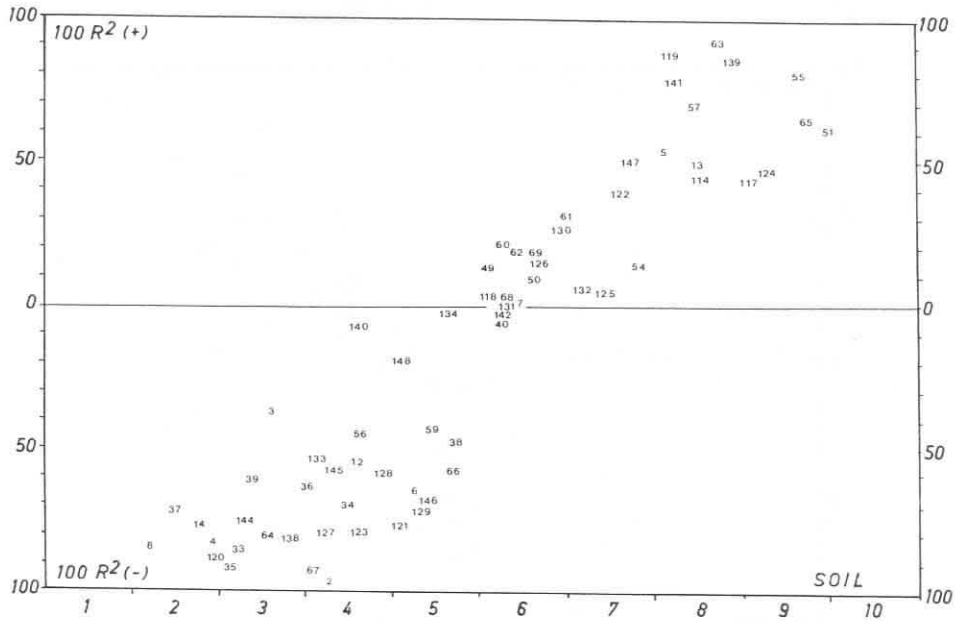

FIG. 2. — The position of the 150 macrofungal species (for identification of number symbols, see Table I) along the integrated variable (SOIL) formed in Figure 1. Each position along the SOIL (X-) axis represents the centre in the distribution of the species. The position along the *y*-axes reports the variability (100 R^2) in the distribution of each species which is accounted for by the SOIL variable. A negative relationship to SOIL is indicated by a position below the 0 line, a positive relationship by a position above this line. Only species belonging to mycorrhiza genera considered.

including *Amanita rubescens*, *Clitocybe clavipes*, *Cl. dealbata/rivulosa*, *Cl. dicolor*, *Collybia butyracea*, *Cortinarius paleaceus/hemitrichus*, *C. anomalus*, *Mycena sanguinolenta*, *Russula nigricans*, *R. ochroleuca*, *Xerocomus chrysentheron*, *Russula fragilis* (oak), *Russula fellea* (beech) and *Lactarius quietus* (oak).

Type B a. — A pronounced maximum at high SOIL values is evident in 25 taxa, including *Agaricus* spp., *Clavulina cristata*, *Coprinus* spp., *Inocybe* spp. (most species of the genus), *Marasmius rotula*, *Russula delica*, *Tricholoma lascivum*, *Lactarius circellatus* (hornbeam), *Mycena crocata* (beech), and *M. pelianthina* (beech).

Type B b. — A less pronounced, not always statistically significant maximum at high SOIL values is demonstrable in 16 taxa. Most frequent are *Armillaria mellea*, *Clitocybe gibba**, *Laccaria laccata*, *Leccinum pseudoscaber* (hornbeam), *Lepista nuda* (mainly oak), *Lycoperdon perlatum**, *Mycena alcalina*, *Mycena pura** and *Omphalina fibula*. The edaphical behaviour of species indicated by * differs between beech and oak/hornbeam forest.

Type C. — A maximum at intermediate SOIL values is only demonstrable in 10-11 species. The most apparent examples are *Collybia confluens*, *Mycena*

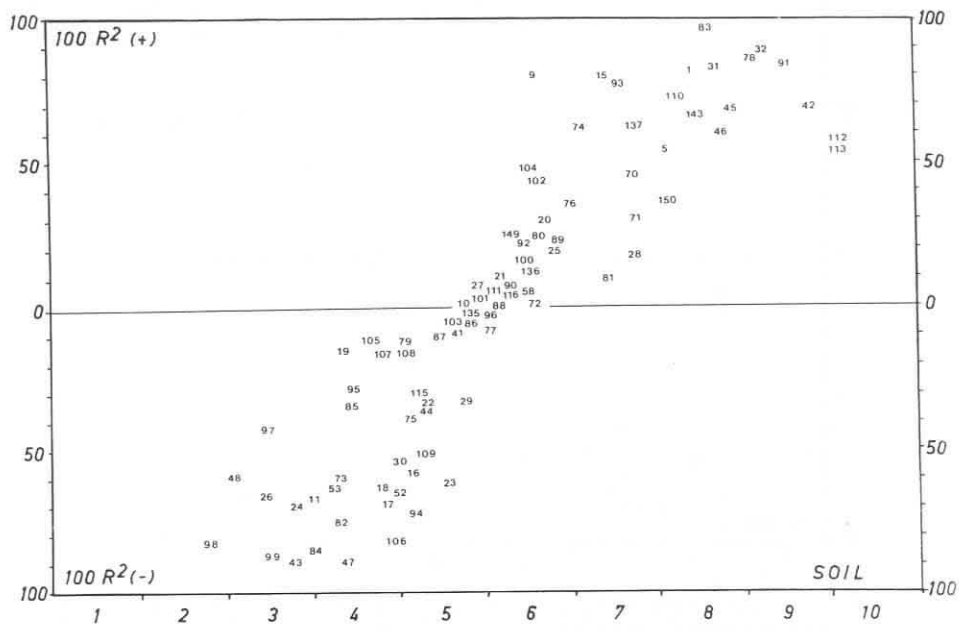

FIG. 3. — The same as Figure 2, but only species belonging to decomposer genera considered.

aurantiomarginata (oak), *Nolanea staurospora*, *Russula vesca*, and *Stropharia aeruginosa*.

Type D. — No distinct maximum, usually a wide edaphical range or sometimes with an irregular distribution in relation to the SOIL variable. About 46 taxa belong to this group. *Mycena vitilis* is ubiquitous and other highly frequent species are *Collybia peronata*, *Mycena galericulata*, *M. galopus*, *M. haematopus*, *Oudemansiella platyphylla*, *Pluteus atricapillus*, *Russula cyanoxantha* and *Xylaria hypoxylon*. However, several less frequent taxa apparently also belong to this type.

The main functional groups of macrofungal species, decomposers and mycorrhiza formers, are almost equally represented in the material as a whole, ca. 70 taxa belonging to genera known or usually believed to form mycorrhiza with forest trees. Among the decomposers, lignicolous taxa are definitely more frequent in the B *a*-B *b* than in the A *a*-A *b* distribution types though also well represented in the D type.

These results were based on qualitative (presence/absence) data. A quantitative consideration of the sporophore formation of the mycorrhiza taxa makes the importance of this functional group in the most acid sites much more obvious (Fig. 5). At low values of the SOIL variable, a mean of ca. 1 200 sporophores ha^{-1} was recorded in an average day during the ten observation seasons (the figure being much higher at maximum sporophore production in September or early October). The comparable number at high SOIL values was ca. 350, to a large extent produced by one species (*Laccaria laccata*) with small sporophores. As opposed to this, however, the probability of finding less frequent or rare species of

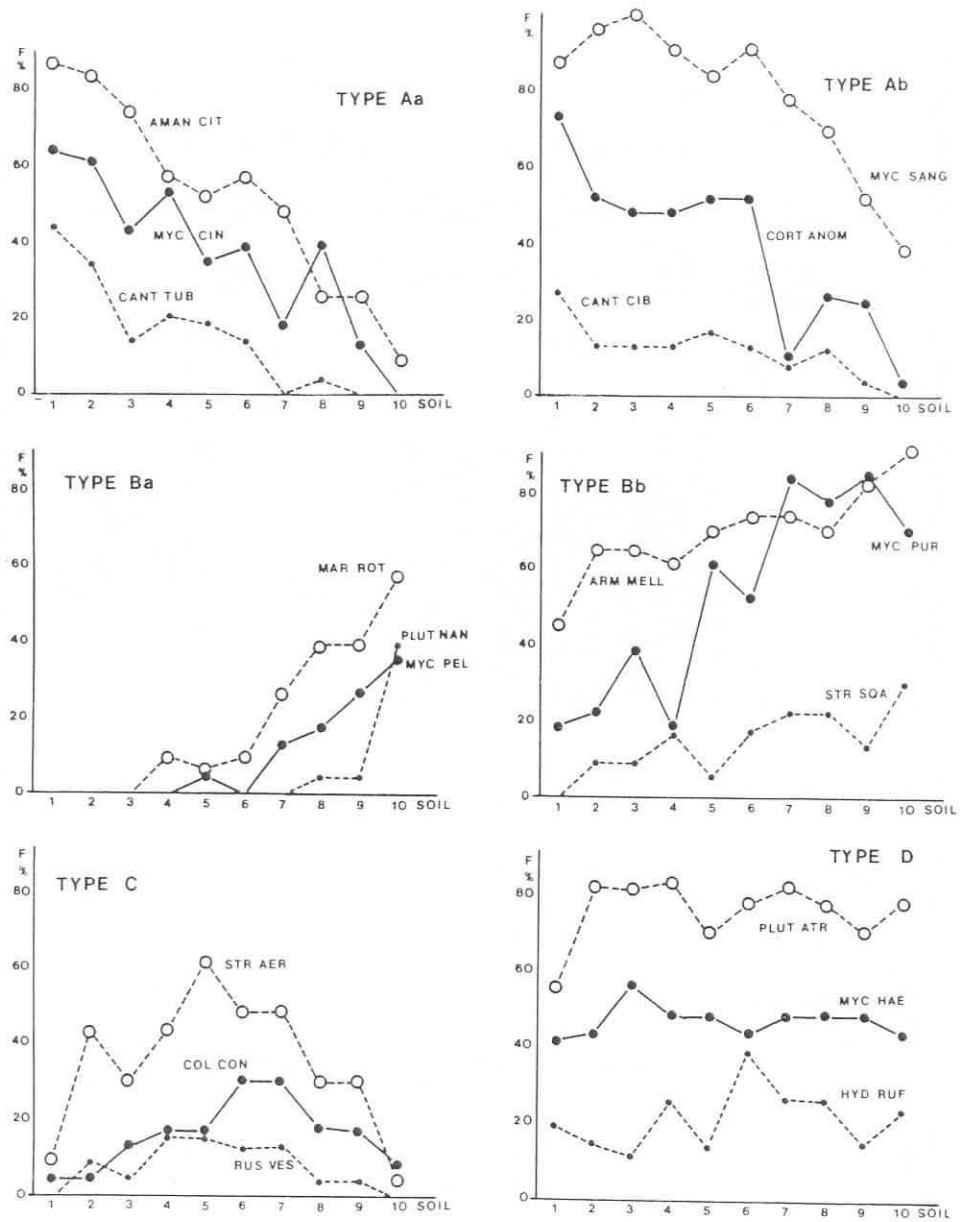

FIG. 4. — The frequency distribution ($F\%$) of selected species along the SOIL axis, arranged in six edaphical distribution types. Type A *a*: *Amanita citrina, Mycena cinerella, Cantharellus tubaeformis.* Type A *b*: *Mycena sanguinolenta, Cortinarius anomalus, Cantharellus cibarius.* Type B *a*: *Marasmius rotula, Pluteus nanus, Mycena pelianthina.* Type B *b*: *Armillaria mellea, Mycena pura, Stropharia squamosa.* Type C: *Stropharia aeruginosa, Collybia confouens, Russula vesca.* Type D: *Pluteus atricapillus, Mycena haematopoda, Hydnum rufescens.*

TABLE I. — *Species/taxa considered* ($n = 150$), *their frequencies and variability of occurrence accounted for* (100 R^2) *by the integrated base saturation-organic matter* (*SOIL*) *variable, classified in ten groups of equal number of sites* (cf. Fig. 1).

Species/taxon no. and name	Frequency %	Centre of distribution on SOIL	Distribution type	% Variability accounted for (100 R^2)	Limitations and comments
1. Agaricus spp.	18	8	Ba	81	
2. Amanita citrina	52	3-4	Aa	95	
3. excelsa/spissa	8	3	Ab	37	
4. fulva	20	2-3	Aa	83	
5. phalloides	15	7-8	Bb	53	
6. rubescens	50	4-5	Ab	64	
7. vaginata	17	6	D	0	
8. virosa	9	1-2	Aa	84	
9. Armillaria mellea	70	6	Bb	80	
10. Calocera cornea	37	5-6	D	0	
11. viscosa	22	3-4	Aa	66	
12. Cantharellus cibarius	12	4	Ab	55	
13. pallens	4	8	Ba	48	
14. tubaeformis	15	2-3	Aa	77	
15. Clavulina cristata	34	7	Ba	79	
16. Clitocybe clavipes	50	4-5	Ab	59	
17. dealbata/rivulosa	63	4-5	Ab	68	c)
18. dicolor	49	4-5	Ab	64	c)
19. fragilipes	15	4	C	14	a)e)
20. gibba	37	6	Bb	29	b)
21. odora	25	5-6	D	8	e)
22. vibecina	56	5	D	33	
23. Collybia butyracea	87	5	Ab	62	
24. cirrhata	38	3-4	Aa	70	c)
25. confluens	16	6-7	C	18	a)
26. cookei	20	3	Aa	67	c)
27. dryophila	74	5-6	D	6	
28. fuscopurpurea	25	7	D	13	d)
29. peronata	77	5	D	33	
30. tuberosa	34	4-5	Ab	57	c)
31. Conocybe tenera	16	8	Ba	82	
32. Coprinus spp.	22	8-9	Ba	86	
33. Cortinarius alboviolaceus	10	2-3	Aa	86	
34. anomalus	39	4	Ab	70	
35. delibutus	18	2-3	Aa	90	d)
36. elatior	12	3-4	Aa	65	
37. flexipes	18	2	Aa	72	a)
38. paleaceus/hemitrichus	69	5	Ab	47	
39. obtusus	11	3	Aa	61	
40. Craterellus cornucopioides	16	5-6	D	1	f)
41. Crepidotus variabilis	74	5	D	7	f)
42. Cyathus striatus	5	9-10	Ba	67	g)
43. Cystoderma amianthinum	40	3-4	Aa	89	
44. charcharias	26	5	D	34	
45. Entoloma nidorosum	12	8-9	Ba	68	
46. rhodopolium	10	8-9	Ba	60	
47. Galerina hypnorum	66	4	Aa	90	
48. Gymnopilus penetrans	13	2-3	Aa	60	
49. Hebeloma crustuliniforme	11	5-6	D	15	
50. Hydnum rufescens	21	6	D	9	
51. Hygrophorus eburneus	17	9-10	Ba	60	a)d)g)
52. Hypholoma fasciculare	46	4-5	Ab	63	
53. sublateritium	33	3-4	Ab	63	
54. Inocybe asterospora	12	7	D	13	
55. geophylla	12	9	Ba	82	a)g)
56. Inocybe napipes	20	4	C-D	45	
57. spp.(excl.napipes)	47	8	Ba	68	c)
58. Kuehnomyces mutabilis	18	6	D	3	
59. Laccaria ametysthina	94	5	Ab-D	44	
60. laccata	90	6	Bb-D	21	
61. Lactarius aurantiacus	18	6-7	Bb-C	31	
62. blennius	56	6	D	18	d)
63. circellatus	33	8	Ba	91	f)
64. camphoratus	33	3	Aa	81	c)
65. fuliginosus	13	9	Ba	65	d)
66. quiletus	94	5	Ab	58	e)
67. theiogalus	60	3-4	Aa	92	c)
68. vellereus	11	5-6	C	2	a)
69. Leccinum pseudoscaber	32	6	Bb-C	19	f)
70. Lepista nebularis	12	7	Bb	44	
71. nuda	23	7	Bb	29	e)
72. Lycoperdon molle	8	6	D	0	
73. nigrescens	30	3-4	Ab	59	
74. perlatum	45	6-7	Bb	61	b)
75. Marasmius androsaceus	31	4-5	Ab	37	e)
76. ramealis	32	6-7	D	33	c)
77. recubans	72	5-6	D	7	e)
78. rotula	18	8-9	Ba	86	
79. Mycena aetites	40	4-5	D	12	c)

Limitations and comments: (*a*) curvilinear relationship lowers the 100 R^2 value; (*b*) edaphical behaviour differs between forest types; (*c*) beechwoods excluded due to incomplete records or low frequency values; (*d*) only beechwood considered due to high preference; (*e*) only oakwood considered due to high preference; (*f*) only hornbeam wood considered due to high preference; (*g*) transformation of frequency variable. Two highly frequent beech forest species were excluded due to incomplete records (*Lactarius subdulcis, Marasmium alliaceus*).

Species/taxon no. and name	Frequency	Centre of distribution on SOIL	Distribution type	% Variability accounted for (100 R^2)	Limitations and comments
80. Mycena alcalina	24	6	Bb	22	
81. aurantiomarginata	14	7	C	7	a)e)
82. cinerella	38	3-4	Aa	76	
83. crocata	47	8	Ba	96	d)
84. epipterygia	36	3-4	Aa	86	e)
85. fagetorum	17	4	Ab	35	d)
86. galericulata	81	5-6	D	5	
87. galopus	66	5	D	11	
88. haematopoda	47	5-6	D	0	
89. inclinata	41	6-7	D	26	e)
90. metata	40	5-6	D	1	
91. pelianthina	10	9	Ba	82	g)
92. polygramma	49	6	D	21	
93. pura	52	7	Bb	77	b)
94. sanguinolenta	79	4-5	Ab	72	
95. stylobates	51	4	D	29	e)
96. vitilis	100	5-6	D	0	ubiq.
97. vulgaris	11	3	Ab	42	e)
98. zephira	8	2-3	Aa	83	
99. Nolanea cetrata	34	3	Aa	87	
100. juncea	36	6	D	16	
101. staurospora	40	5-6	C	0	
102. Omphalia fibula	39	6	Bb	43	c)
103. Oudemansiella platyphylla	68	5	D	4	
104. radicata	85	6	D	47	d)
105. Panellus stypticus	18	4-5	D	11	e)
106. Paxillus involutus	49	4-5	Ab	82	
107. Phallus caninus	11	4-5	D	16	
108. impudicus	42	4-5	D	16	
109. Pholiota lenta	42	5	Ab	52	
110. marginata	13	7-8	Ba	71	
111. Pluteus atricapillus	76	5-6	D	4	
112. nanus	5	10	Ba	54	a)g)
113. salicinus	5	9-10	Ba	56	a)g)
114. Porphyrellus porphyrosporus	13	8	Ba	43	d)
115. Psathyrella hydrophilum	34	5	D	31	
116. Psilocybe crobula	9	5-6	D	2	
117. Russula alutacea/olivacea	8	8-9	Ba	43	
118. cyanoxantha	57	5-6	D	0	
119. delica	22	7-8	Ba	87	
120. Russula densifolia	11	2-3	Aa	89	
121. fellea	77	4-5	Ab	77	d)
122. foetens	19	7	Bb	39	d)
123. fragilis	58	4	Ab	80	e)
124. graveolens	5	9	Ba	44	
125. heterophylla	16	7	C	4	a)d)
126. lutea	20	6	D	16	
127. mairei	57	3-4	Aa	78	d)
128. nigricans	56	4-5	Ab	59	
129. ochroleuca	73	4-5	Ab	72	
130. rosacea	8	6-7	D	26	
131. rosea	23	5-6	D	2	d)
132. sororia	13	7	C	6	a)e)
133. velenovskyi	17	3-4	Ab	55	c)
134. vesca	8	5	C	2	a)
135. Stropharia aeruginosa	35	5-6	C	2	a)
136. cyanea	37	6	D	10	f)
137. squamosa	14	7	Bb	62	
138. Tricholoma columbetta	8	3-4	Aa	81	
139. lascivum	22	8-9	Ba	84	
140. sciodes	21	4	D	7	d)
141. sulphurea	11	7-8	Ba	78	
142. ustale	18	5-6	D	0	d)
143. Tubaria furfuracea	17	8	Bb	66	
144. Tylopilus felleus	13	3	Aa	76	
145. Xerocomus badius	17	3-4	Ab	58	
146. chrysentheron	80	5	Ab	67	
147. porosporus	17	7	Bb	49	c)
148. subtomentosus	17	4-5	D	18	e)
149. Xylaria hypoxylon	80	6	D	23	
150. polymorpha	17	7-8	Bb	35	f)

The following species were classified as mycorrhiza taxa (belonging to mycorrhiza genera):
Nos. 2-8, 12-14, 33-40, 49-51, 54-57, 59-69, 106, 108, 114, 117-134, 138-142, 144-148.

Distribution types with respect to the SOIL variable: A *a.* Pronounced maximum at low (1-3) SOIL values. Often not even observed at SOIL 8-10. A *b.* Less pronounced maximum at low SOIL values. B *a.* Pronounced maximum at high SOIL (8-10) values, often not even observed at SOIL 1-3. B *b.* Less pronounced maximum at high SOIL values. C. Maximum at intermediate (4-7) SOIL values. D. No distinct maximum; usually with a wide range with respect to SOIL.

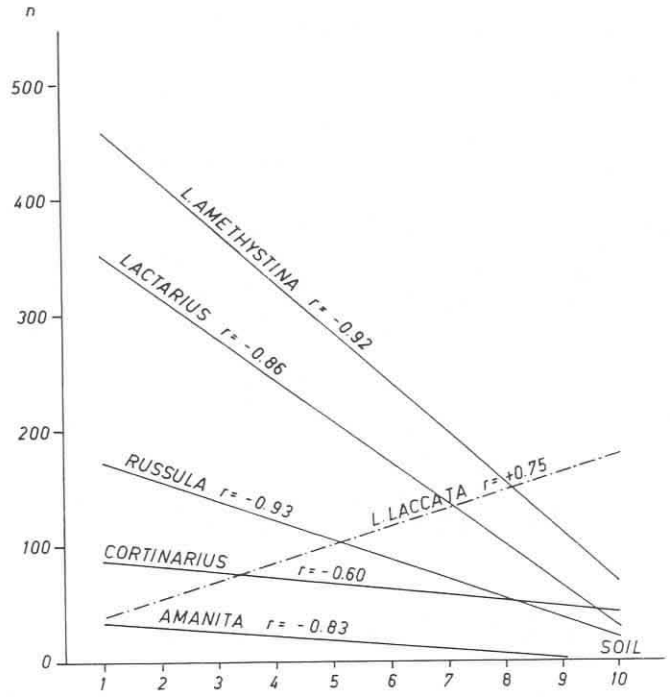

FIG. 5. – Regression lines on the SOIL variable for the mean number of sporophores (ha^{-1} observation $date^{-1}$) of main mycorrhiza genera/species.

mycorrhiza genera, not included in Table I, has proved to increase with increasing value of the SOIL variable.

There is a negative correlation ($r = -0.87$, $p < 0.001$) between the total number of species recorded per 500 m^2 and the classified SOIL variable. Species sums do not differ greatly, however, on average being 60 and 51, respectively at the extreme ends of the variable. Almost no relationship ($r = -0.10$) was detected between the total number of mycorrhiza and decomposer species recorded per observation plot in the material as a whole.

A closer examination of the importance of the quantity and species composition of the understorey vegetation to the macrofungal differentiation is outside the scope of this paper. However, preliminary evidence suggests that interrelations are usually weak or far from clear cut. A few decomposer taxa display decidedly different ranges in beech and in oak/hornbeam forest with respect to the SOIL variable. These taxa are *Agaricus* spp., *Lycoperdon perlatum*, *Mycena pura* and, in particular, *Clitocybe gibba* (Fig. 6). In beech forest, the total ranges of these species are almost congruent with the upper half or even upper third of the SOIL variable. In forests dominated by oak or hornbeam their ranges are considerably wider, though usually not including the mor part of the SOIL variable. The generally less abundant field-layer vegetation under beech, except at the least acid sites, resulting

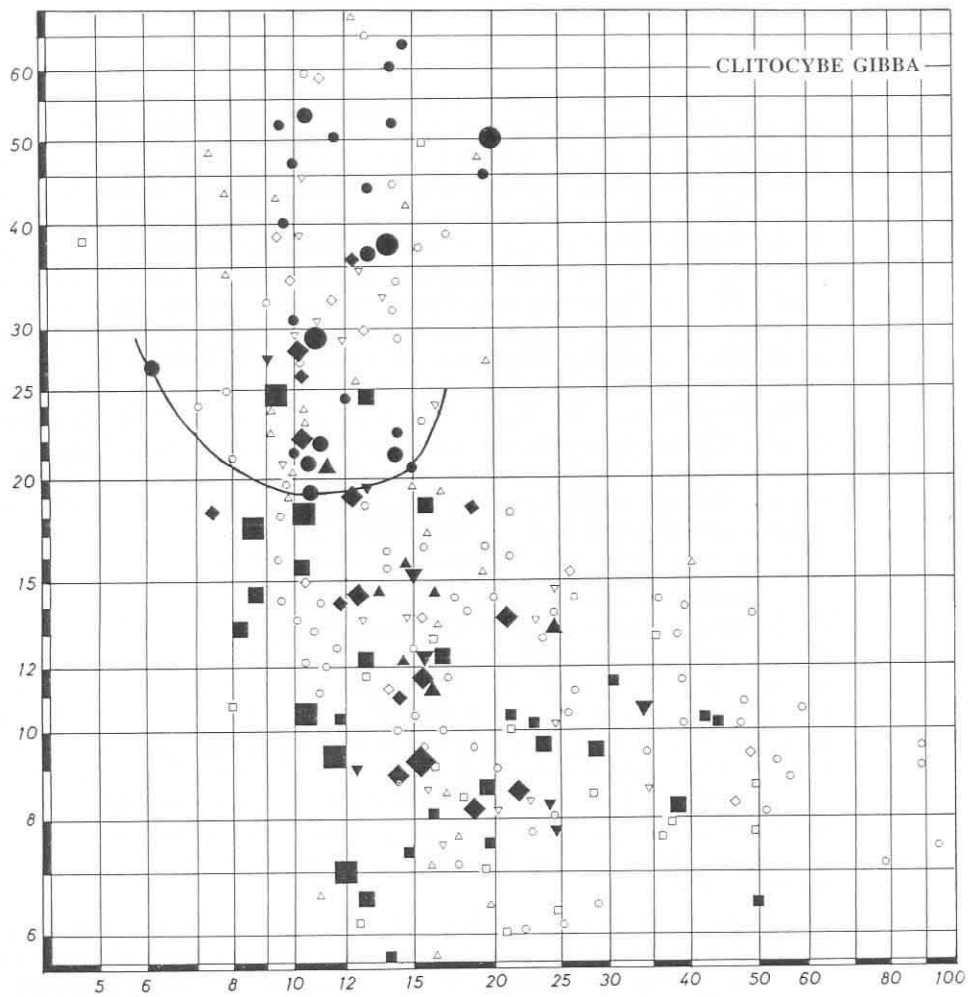

FIG. 6. – In a few taxa the edaphical preference differs conspicuously between forest types. With beech wholly dominating the tree layer, the edaphical range of *Clitocybe gibba* is much more narrow (no occurrences below the line) than in oak and oak/hornbeam forest. For further explanations, see Figure 1.

in a less diversified litter quality, seems to be related to this discrepancy. A closer examination of the primary data, however, revealed some obvious deviations from this rule and other environmental factors than general soil properties and litter quality should also be considered. It is possible, though not wholly likely, that beech forest populations of the species in question may differ ecophysiologically or taxonomically from populations encountered with oak or hornbeam.

DISCUSSION

This study was based on observations in 228 permanent plots, each 500 m^2, 10-15 times during the main season of sporophore production in 3-5 (usually 4) years and as a whole extended over a period of 10 years. The importance of observation frequency and duration for determining the "complete" species composition of a site has sometimes been discussed in the mycological literature. According to KALAMEES (1968) at least 2 seasons of frequent observation of a forest stand is necessary for a reasonably complete list. In Juniper scrub studied by BARKMAN (1987) 60% of the species were found in 4 years and 89% in 8 years. Also with a considerable number of observation times there will always be an appreciable share of species encountered only once (cf. HACK, 1983). This list of "occasional" taxa may be composed both of species which fruit very rarely and of species which really occur in very few places. In a regional 5-year study of 30 hornbeam stands (TYLER, 1989 *b*), where the vascular plant and the macrofungal species composition were compared, the share of "only once" species was only slightly higher for the macrofungi. Immigration of occasionally successful but probably most often ephemeral diaspores from surrounding ecosystems will constitute an appreciable share of such "only once" species in various organism groups.

The two variables used for edaphical characterization, the base saturation and the organic matter content of the humus layer, are well suited for characterizing the mor-mull direction of variation of forest soils. Moreover, they closely reflect the pH conditions of the soils. Experimentally, the pH of the growth medium has proved to be related to the performance of various species. Most mycorrhizal taxa tested in pure culture have shown maximum mycelial growth at pH 4-6, though there are apparent exceptions (SLANKIS, 1974). Already GRAINGER (1946) concluded that macrofungi have definable preferences for particular pH ranges of the substrate. In several studies (e. g., RICEK, 1980) the species have been coarsely classified as "neutrophilous", "acidophilous", etc., though the basis of the classification is rarely documented.

BOHUS & BABOS (1960), however, did not consider pH important for the distribution of vascular plants and fungi in deciduous forest. It is sometimes evident that a taxonomically defined species may contain strains characterized by highly different pH optima. So is the case in *Paxillus involutus* (cf. SLANKIS, *op. c.*). In the beech forest of south Sweden this species seems to occur mainly or exclusively as a decomposer in the most acid soils (TYLER, 1984), whereas with hornbeam, it is widespread and probably a mycorrhiza former even in plantations on calcareous clay.

To some or even a great extent, the importance of pH for macrofungal differentiation may be mainly of an indirect nature. Low pH usually means a low supply of exchangeable base cations and other soil nutrients and a high solubility of certain trace metals and aluminium, a nitrogen turnover ending up in ammonium, not in nitrate, etc. Therefore, soil pH or other soil acidity functions, e. g., base saturation, should primarily be considered a property valuable for characterizing the general chemical state of a soil, though it cannot be excluded that the hydrogen ion activity per se may also be of a direct importance to the edaphical differentiation of macrofungi.

The importance of organic matter to heterotrophic organisms can never be overestimated. Amount and character of the litter produced set the ultimate limits for the distribution of all decomposer taxa, just as the occurrence of suitable trees sets these limits for many mycorrhiza species. From Figures 2-4 and Table I, however, it is evident that most species do not occur within the entire ecological range determined by these superior factors. The extreme ends of the soil variable defined and considered in this study support quite different macrofungal floras. Apart from differences in the inorganic soil chemistry discussed above, differences in the organo-chemical properties of the litter and humus might be of importance. The litter produced by the same tree species in the most acid (mor) sites differs in several respects from that produced in typical mull sites. It is probably richer in phenolic compounds, also shown to be more toxic at low pH (HINTIKKA, 1982) and this might be of considerable significance. Even mycorrhiza species, mainly dependent on the tree host for organic nutrition, react differently on organic compounds. Quantity and type of humus may be decisive factors for mycorrhiza formation according to MEJSTRIK & DOMINIK (1969). Organic matter was considered a key factor governing ectomycorrhizal activities in forest soils, though mainly owing to its ability to buffer wide variations of pH, moisture and temperature (HARVEY *et al.*, 1980).

A close examination of Figure 3 reveals that even the distribution of wood or bark decomposing fungi may be highly dependent on soil properties. *Pluteus nanus*, *Pluteus salicinus*, *Mycena crocata* and *Marasmius rotula* occur exclusively in sites with mull properties, primarily at high base saturation values, whereas *Gymnopilus penetrans* decomposes beech and oak wood in the most acid sites. Decomposers characterizing earlier stages of wood decay are usually less particular about soil properties. At the decomposition, wood becomes increasingly permeable to, e. g., minerals and acids contained in the throughfall water, the composition of which varies considerably between sites, partly according to soil conditions (BERGKVIST *et al.*, 1987). There may also be differences in the throughfall contents of sugars and other organic compounds due to variability in leaf contents between sites (BALSBERG, 1989). Formation of a soil mycelium may enable the wood decomposer to amend a nutrient-deficient substrate by enclosing macronutrients from the soil and some passive nutrient diffusion from soil into surface litter may also occur (GRAMSS, 1980). Aerially exposed wood may be occupied predominantly by species colonizing by spores, while wood in ground contact contain species colonizing by mycelium (CARRUTHERS & RAYNER, 1979).

It is apparent from the results that the edaphical preference often differs greatly between species belonging to the same taxonomical genus, though notable exceptions do exist. All species of *Agaricus* and *Coprinus* and by far the great majority of *Inocybe* are exclusively to be found on mull soils, preferably at high base saturation values. Most of the numerous *Cortinarius* taxa, on the contrary, are more frequent or restricted to the very acid soils, usually those high in organic matter. The many *Cortinarus* (*Phlegmacium*) taxa known to occur in deciduous woodland on calcareous soils are almost lacking in Scania.

It is remarkable that only a few (7%) of the 150 most common species in the Scanian deciduous forest have their frequency maxima in the intermediate part of the SOIL range (distribution type C in Figure 4). Instead, more than half (57%) of all taxa display maxima either at 1 or at 10 on the SOIL scale, i. e. partly or

most likely outside the wide edaphical range realized. About one third of all taxa seems more or less unrelated to the edaphical variability realized (distribution type D) and are likely to have an even wider ecological potential. From a theoretical point of view, the scarcity of type C taxa may indicate that conditions prevailing in most forest soils today represent unstable transitional stages between calcareous mull and very acid mor. Most taxa occurring in the Scanian deciduous forest have probably developed under either of these two extremes and few taxa seem to have had the possibility to develop preference for the "transitional" stages.

As previously observed in other field studies (e. g. HERING, 1982) the production of sporophores, mainly of mycorrhizal taxa, was definitely higher at low than at high SOIL values during this 10-year period of observation. This is consistent with the classical theory that ectomycorrhiza of forest trees is favoured by a certain shortage of, i. e., soil mineral nutrients (BJÖRKMAN, 1949), supposed to be characteristic of podzolic soils. Of the numerous species belonging to mycorrhiza genera, however, only few of them contribute significantly to the number of fruitbodies produced in all or most sites. In fact, the number of species belonging to mycorrhiza genera is often higher in certain mull soils, though most of them are characterized by a scanty sporophore production.

CONCLUSIONS

The macrofungal flora of the south-Swedish deciduous forest is composed of taxa characterized by great differences in their response to properties of the soil. Slightly more than half of the 150 most frequent species display distribution maxima either in the most acidic mor soils or in well-developed mull soils at a high base saturation. Quite few taxa are most frequent in sites with intermediate soil characters (presently the dominating soil types in south Sweden), whereas about one third of the taxa seems more or less unrelated to the edaphical variability and is probably characterized by an even wider edaphical range. Species with distinct frequency maxima or an exclusive occurrence at either end of the edaphical range are found in all functional groups (humus-dwelling, surface litter and wood decomposers as well as mycorrhiza species). The sporophore production of most mycorrhiza taxa is distinctly higher in the very acid soils, particularly in the mor podzols.

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